Manipulation of host behavior and host-associated diversification in strepsipteran insects(Digest_要約)

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Digest

Title

Manipulation of host behavior and host-associated diversification in strepsipteran insects

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Strepsipterans are unique parasitic insects in that the free-living first instar larvae search and invade their host by themselves, in contrast to many other insect parasitoids whose free-living females search for hosts and lay their eggs on or in them. One of the most characteristic features of strepsipteran life is the extreme sexual dimorphism, whereby adult males and females share no external morphological characters. The adult males are free living, but adult females (except Mengenillidia) remain endoparasitic in their host throughout their life. Only the cephalothorax of females is visible externally, and the rest of the cylindrical body stays within the host and is devoid of all adult insect characters. The morphological degeneration in adult females causes difficulty in the classification of strepsipterans.

Strepsipteran females often manipulate the behavior of their hosts to maximize their own fitness by improving the host survival rate or by enhancing the parasitism success of their offspring. This thesis examined four families of strepsipterans and studied their life history and population dynamics (Chapter 2), reported the manipulated behavior of parasitized bees (Chapter 3), and unveiled the diversity and host specialization of strepsipterans based on molecular and morphological information (Chapter 4, 5, 6).

Chapter 1

General introduction

The unique parasitic life of the order Strepsiptera is reviewed. The order Strepsiptera consists of 10 families and approximately 600 species, and

parasitizes seven orders and 33 families of Insecta. Strepsipterans undergo dramatic remodeling of body structures in the course of ontogeny (polymetabolic development). Free-living males actively fly using their hind-wings. They are also known for their short lifespan of several hours only. Females release powerful sex pheromones to attract males for mating. The eggs develop to the first instar larvae within the female body and are released from the brood canal that opens into the cephalothorax of the female. Since the first description of a strepsipteran in 1793, the phylogenetic position of the order Strepsiptera has been debated, the so-called "Strepsiptera problem." Historically, the phylogenetic position of Strepsiptera has changed many times, although in recent studies, Strepsiptera has been placed as a sister group of the Coleoptera or included in the Coleoptera. The Strepsiptera problem has not yet been resolved. In the order Strepsiptera, a Hymenoptera-associated group has highly diversified and most species have known host species. Therefore, Hymenoptera-associated strepsipterans enable us to explore the process of the host-associated diversification of strepsipterans.

Chapter 2

Life history and host utilization pattern of a strepsipteran parasite (Insecta: Strepsiptera) on blissine bugs (Hemiptera: Lygaeidae) living under dwarf bamboo leaf sheaths

The blissine bug *Macropes obnubilus*, which lives aggregately under the leaf sheaths of the evergreen dwarf bamboo, is parasitized by the strepsipteran parasite *Blissoxenos esakii*. To detect the ecological properties of the bug–strepsipteran system, I conducted field surveys on the population dynamics of *Macropes* bugs and their *Blissoxenos* parasites. The parasitism rate of the strepsipteran was high throughout the year and was significantly higher in female than in male bugs. *Blissoxenos* adult males emerged mainly in May, and neotenic adult females released triungulins in August. The triungulins invaded host nymphs, but subsequent larval development did not

occur before the bugs matured. At most two strepsipterans could mature in a host because of spatial limitations. The mortality of triply or more parasitized bugs was significantly higher than that of singly or doubly parasitized bugs, which survived longer than uninfected ones. The heavy strepsipteran infection profoundly affected the host population dynamics by causing host reproductive failure.

Chapter 3
Bee-parasitic strepsipterans adaptively manipulate hosts' flower-visiting behavior

The manipulation of host behavior by parasites is considered to maximize parasites' fitness and is widespread among various invertebrate parasites. Here I report a new type of manipulation of host behavior in a bee-parasitic strepsipteran, *Halictoxenos borealis* (Stylopidae). The host bee species, *Lasioglossum apristum* (Halictidae), is a eusocial species and workers frequently visit *Hydrangea serrata* flowers to collect pollen. The bees parasitized by the strepsipteran, however, did not show pollen collection behavior but bent their abdomen downward and pressed the dorsal tergites of their abdomen onto the flowers. Extensive examination of *Hydrangea* inflorescences detected the presence of released strepsipteran larvae. These results indicate that the manipulation of host behavior may help the strepsipteran to release its larvae onto flowers and to increase the chance of phoresy onto flower-visiting host bees.

Chapter 4
Species diversity and host specialization in the family Stylopidae (Strepsiptera)

Because of the scarcity of morphological characters, classifications of Strepsiptera, especially in the bee-associated family Stylopidae, have been dubious. To clarify the species criterion and extent of host-specificity of the bee-parasitic family of Strepsiptera, Stylopidae, molecular phylogenetic

analyses were conducted. By sequencing the mitochondrial genes (COI) and nuclear genes (18S ribosomal DNA) of 34 strepsipterans collected from 25 host species, a maximum likelihood phylogenetic tree was obtained. The phylogenetic tree supported the monophyly of the two genera *Halictoxenos* and *Stylops*, which are respectively associated with halictid and andrenid bees. Morphological examination accompanied with DNA barcoding demonstrated that *Halictoxenos* strepsipterans that associated with different host species were different species, but that many *Stylops* species are associated with multiple host species. This suggests that host-specificity was high in *Halictoxenos* but not in *Stylops*. In *Halictoxenos*, eusocial bees were used as hosts significantly more frequently than solitary bees, whereas all andrenid hosts of *Stylops* were solitary. This suggests that the eusociality of host bees causes high host-specificity of strepsipterans.

Chapter 5
Cryptic diversity and host specificity in giant *Xenos* strepsipterans parasitic in large *Vespa* hornets

Xenos is a strepsipteran genus whose members are parasitic to eusocial vespid wasps, including the hornet genus *Vespa*. To clarify the diversity of *Xenos* strepsipterans associated with hornet species, I performed molecular phylogenetic analyses of *Xenos* strepsipterans based on mitochondrial cytochrome *c* oxidase subunit I gene sequences (652 bp). The analyses, accompanied by morphological examination, revealed that these strepsipterans are comprised of two distinct species, *X. moutoni* du Buysson, 1903 and *X. oxyodontes* sp. nov. The two species differed in their host-utilization pattern; the latter was mostly specific to *Vespa analis* and *V. simillima*, whereas the former was associated with other *Vespa* species.

Chapter 6
A new species of the genus *Tridactylophagus* (Strepsiptera, Halictophagidae) from Kyoto, Japan

Tridactylophagus etoi sp. nov. was described from female specimens parasitic to tridactylid pygmy mole crickets, *Xya japonica* (Haan, 1842) collected at Tango, Kyoto, Japan. It is the first record of *Tridactylophagus* from Japan. Morphologically, the new species resembles *T. coniferus* (Yang, 1964) recorded from China, but can be easily distinguished from the latter by the shape of its cephalothorax, position of spiracles, and other morphological characters.

Chapter 7
General discussion

In Chapter 7, I provide a general discussion of strepsipterans. Physiological and behavioral manipulations of hosts by endoparasitic females were widespread among various strepsipterans, probably because the probability that first instar larvae released from females could find and reach their host is very low and can be enhanced by the manipulations. These intimate interactions between strepsipterans and their hosts influence the process of diversification in strepsipterans. The molecular phylogenetic analyses and morphological observation of female cephalothoraxes clarified that a traditional taxonomy based on female morphology is largely correct and that host-specificity was very high (in *Halictoxenos*-associated eusocial bees) or moderate in strepsipterans associated with solitary bees and eusocial wasps. These results contribute to our understanding of the process of host-associated diversification in strepsipterans.